

THE UNUSUAL OCCURRENCE OF AQUATIC BEETLES IN AMBER,
COPELATUS APHRODITAE BALKE, N. SP. AND *C. PREDAVETERUS* MILLER,
N. SP., (COLEOPTERA: DYTISCIDAE: COPELATINAE)

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Abstract.—*Copelatus aphroditae* Balke, new species, is described based on a single female from Baltic amber (Eocene), and *C. predaveterus* Miller, new species, is described from five specimens preserved in Dominican amber (late early Miocene to mid-Oligocene). The former does not fit into previously defined species groups and is assigned to the new *C. aphroditae*-group. *Copelatus predaveterus* is assigned to the *C. trilobatus*-group which currently contains at least 20 extant species and has, in aggregate, a Pan-tropical distribution. The discovery of these specimens is interesting since aquatic beetles are relatively rare in fossil tree resins. Also, they are very similar to derived extant *Copelatus*, suggesting relatively prolonged stasis in the morphology of this very speciose genus (>430 described species). Based on these specimens, *Copelatus* is at least 50 million years old and at least some of the species groups are perhaps 30 million years old.

Key Words: water beetle, Baltic and Dominican amber, phylogeny, fossil insects

Despite considerable interest in amber-preserved insect specimens, few diving beetles (Dytiscidae) have been reported from amber. This seems reasonable since aquatic beetles are seemingly unlikely candidates for preservation in tree resins. Nevertheless, the unusual occurrence of a few adult and even some larvae of aquatic adephagan beetles in amber has been mentioned including specimens of Gyrinidae (Hatch 1927; Helm 1896; Keilbach 1982; Menge 1856; Motschulsky 1856; Weitschat and Wichard 1998; Wichard and Weitschat 1996) and Dytiscidae (Berendt 1845; Helm 1896; Keilbach 1982; Poinar 1992; Poinar and Poinar 1999; Spahr 1981a, b; Weidner 1958; Weitschat and Wichard 1998; Wichard and Weitschat 1996; Wunderlich 1986), though many of these refer to the

same specimens. The only species of Dytiscidae described from amber so far is *Glesseria rostrata* Koch and Berendt, 1845. This species is based on a single larva in Baltic amber and was originally assigned to Thysanura, not Coleoptera, albeit with some doubt (Handlirsch 1908; Koch and Berendt 1854).

Diving beetles are a comparatively well-studied family taxonomically, and the group is becoming better known phylogenetically (e.g., see Miller 2001). Despite this and despite the usefulness of fossils for providing unique character combinations and determining minimum ages of divergences, relatively little effort has been placed on the study of fossil dytiscids. Because diving beetles are aquatic, the chance of fossilization of specimens in sediments is probably

higher than for many other insects. The literature does, in fact, contain many references to fossilized dytiscids (mainly impression fossils), but these are often described in only limited detail with very little evidence offered for their taxonomic placement. The numerous dytiscid (and other hydradephagan) fossils available in collections are a potentially large, untapped source of information about the evolution of the group. Though amber specimens of Hydradephaga are certainly much more rare than impression fossils, at least several comparatively well-preserved adult specimens of *Copelatus* Erichson are available for study and are described herein. These are the first species of Dytiscidae described from adult specimens in amber.

Copelatus is one of four genera of Copelatinae and is the most speciose genus of Dytiscidae (433 described species; Nilsson 2001) with most of its members occurring in the tropics. The genus has never been completely revised and is in need of a detailed cladistic analysis with broad taxon and character sampling in addition to considerable species-level monographic work. Extant species in the group are usually separable on the basis of male genital structure, as well as coloration and fine structural details of the cuticle, all of which are difficult or impossible to examine in amber preserved specimens. Nevertheless, the species described here appear to possess external character state combinations sufficient for diagnosing them from extant taxa. Here, we describe two new species which belong to the extant genus *Copelatus*, *C. aphroditae* Balke from Baltic amber, and *C. predaveterus* Miller from Dominican amber.

MATERIAL AND METHODS

Figures.—Line drawings of *C. predaveterus* and *C. aphroditae* were created with the aid of drawing tubes on a Wild M3C and a Leitz MZ12 dissecting microscope, respectively.

Preparation and condition of specimens.—Specimens of *C. predaveterus* were

prepared with methods described by Grimaldi (1993). They were examined by placing the amber piece on a drop of glycerine on a microscope slide. A drop of glycerine was then placed on the dorsal surface of the amber piece and a coverslip placed over the drop. The entire piece containing *C. aphroditae* was placed in a small tray with glycerine and then examined.

Measurements.—Measurements of *C. predaveterus* and *C. aphroditae* were made using ocular scales in a Wild M3C and a Leitz MZ12 dissecting microscope, respectively. Some of the specimens are distorted by compression or stretching in the amber, but measurements do not correct for this in any way. For this reason, measurements are unavoidably inaccurate and give only a general idea of the actual dimensions of most of the specimens. Total length (TL) and greatest width (GW) are provided along with the ratio TL/GW to provide an indication of shape.

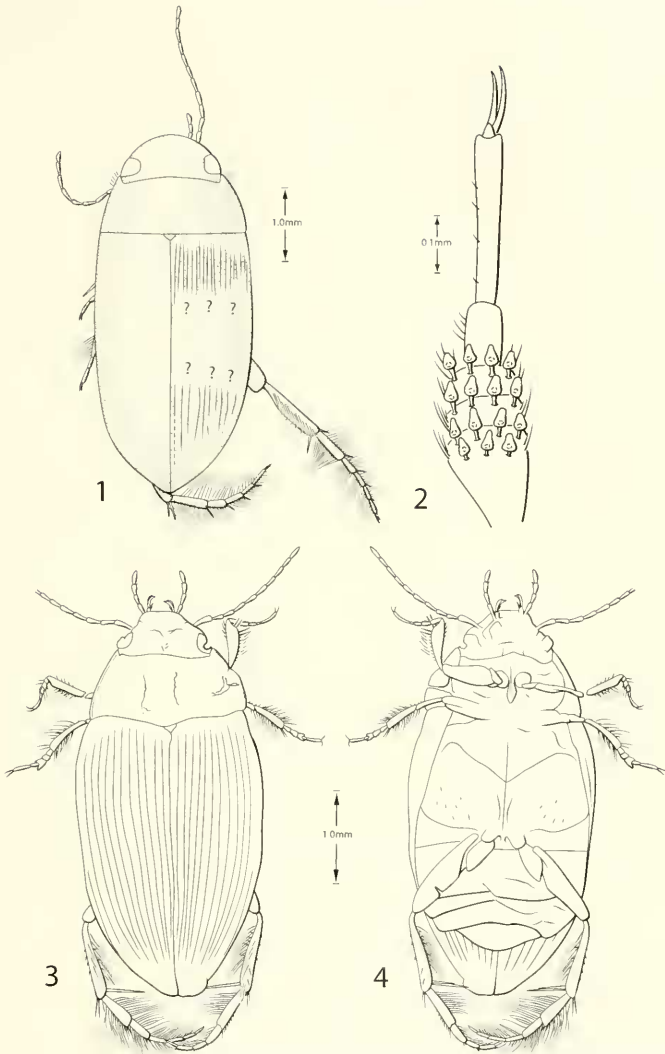
Copelatus aphroditae Balke, new species (Fig. 1)

Holotype.—♀, in collection A. Herrling, Bramsche, Germany, labeled # 1153. The piece is clear, yellowish golden. The beetle is partly covered with a whitish film of air. Besides the beetle, there are two pieces of sclerotized, cuticular material in the amber, which could not be identified. Also, there are few "Sternhaare," which are thought to be minute parts of oak trees and which are characteristic of the Baltic Amber (Weitschat and Wichard 1998).

Diagnosis.—With 19 discal striae on elytron anteriorly; posteriorly with ten striae visible. Submarginal stria absent (Fig. 1); size small (total length 5.0 mm); body in dorsal view approximately parallel-sided (Fig. 1).

Description.—*Measurements*: TL = 5.0 mm; GW = 2.2 mm; TL/GW = 2.27.

Dorsal side (Fig. 1): Elongate, lateral margins continuously curved between pronotum and elytron. Body approximately parallel-sided in dorsal view. Head (partly



Figs. 1-4. 1, *Copelatus aphroditae*, holotype ♀, dorsal habitus. 2-4, *C. predaveterus*. 2, Male protibia, ventral aspect. 3-4, Holotype ♀, habitus. 3, Dorsal. 4, Ventral.

crushed) with distinct microreticulation (MR) of honeycomb-like cells; with few larger punctures, their diameters equal to that of meshes. Pronotum with MR of regular, slightly longitudinally-oriented cells, with few larger and smaller punctures; discally with short striae which increase in length and depth laterally. Pronotum with lateral bead complete, extending nearly to anterior angle. Elytron with 19 longitudinal striae, with only 10 striae visible on posterior portion of elytron; without submarginal stria. With MR and relatively dense punctation between the striae.

Ventral side: Prosternal process moderately convex, apex narrowly rounded. Metasternum with MR of horizontally oriented cells; metacoxa with MR of cells in diagonal orientation, few larger punctures and with diagonal striae. Metacoxal lines closely approximated posteriorly. Ventrites 1–5 chagreened and with few larger punctures; with oblique striae on ventrite 1 becoming increasingly transverse posteriorly. Last visible sternite without lateral striae.

Etymology.—Named after Aphroditae, Greek god of love.

Occurrence.—Baltic Amber, Eocene.

Comments.—This species does not fit well into other, currently-recognized species groups, and we assign it to a new *Copelatus aphroditae*-group based on the presence of nineteen discal impressed striae on the elytron and the lack of a submarginal elytral stria.

Copelatus predaveterus Miller,
new species
(Figs. 2–4)

Type specimens.—Holotype, ♀, AMNH DR-14-615, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-14-615 Locality:/Copelatus trilobatus-group Det AN Nilsson-96/HOLOTYPE *Copelatus predaveterus* Miller 2000."

Paratypes (4): 1 ♂, AMNH, same amber piece as holotype, same labels; 1 ♂, AMNH DR-14-974, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-

14-974 Locality:": 1 ♀, AMNH DR-14-973, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-14-973 Locality:/Amber: Oligo-Miocene Dominican Republic: mines at or near La Toca AMNH (no cat. no. yet)/DYTISCIDAE COPELATUS SP. det. PJ Spangler": 1 ♀, AMNH DR-14-616, labeled, "AMBER: Oligo-Miocene Dominican Republic AMNH no. DR-14-616 Locality:/Copelatus trilobatus-group Det AN Nilsson-96."

Although male specimens of Dytiscidae are generally selected as holotypes, a female specimen was selected since this individual is easily visible dorsally and ventrally, and the piece of amber in which it is included also contains a male specimen, which is currently less visible, but which, in the future, will be easily associated with the female holotype. The only other male specimen is the least distorted of the specimens and is also easily visible. However, it is on the extreme edge of the amber piece where this piece is broken, and some of the specimen is exposed to the air. Parts of the legs and antennae are in the piece that is broken off. Rather than selecting this specimen, which is in more tenuous condition, a specimen was chosen that is well within a relatively strong piece of amber and is entirely intact.

Diagnosis.—Eleven discal and one submarginal striae present on elytron, first stria not shortened, of similar length to others (Fig. 3); size small (total length 3.8–4.4 mm); male pro- and mesotarsal claws unmodified (Fig. 2); male without striae on pronotum.

Description.—*Measurements:* TL = 3.82–4.40 mm; GW = 1.84–2.36 mm; TL/GW = 1.79–2.21.

Dorsal side: (Fig. 3). Elongate oval, lateral margins continuously curved between pronotum and elytron. Male apparently without distinct striae on pronotum or elytra. Pronotum with lateral bead complete, extending nearly to anterior angle. Elytron with 11 discal and 1 submarginal striae; all

discal striae elongate and distinct, not shortened (Fig. 3).

Ventral side: (Fig. 4). Prosternal process moderately convex, apex narrowly rounded (Fig. 4). Male pro- and mesotarsal claws not modified (Fig. 2). Male pro- and mesotarsomeres 1–3 moderately expanded, ventrally with 4 rows of adhesive setae (Fig. 2), 2 rows on tarsomere 1, 1 row on 2, and 1 row on 3, most proximal row with 3 adhesive setae, other rows with 4 adhesive setae. Male pro- and mesotibiae not modified.

Etymology.—This species is named *predaveterus* from the Latin *preda*, meaning “predator” and *veterus*, meaning “of a former time” in reference to the carnivorous habits and ancient existence of this species.

Occurrence.—Dominican amber, Oligocene-Miocene, Dominican Republic.

Comments.—This species is a member of the *Copelatus trilobatus*-group (*sensu* Guéorguiev (1968)) based on the presence of eleven discal and one submarginal impressed striae on the elytra. Within this group, it may be distinguished from most of the species by its smaller size. Other species in the group similar to *C. predaveterus* in size are *C. concolorans* Balfour-Browne, *C. gschwendmeri* Guignot, *C. perfectus* Sharp, *C. trilobatus*, Régimbart and *C. undecimstriatus* Aube, and members of most of these species are still generally larger than *C. predaveterus*. *Copelatus predaveterus* has unmodified male prostarsal claws, has the first elytral stria elongate (not shortened) and males apparently lack striae on the pronotum, though fine details of cuticular surfaces are not easy to discern on these specimens. Based on these features, *C. predaveterus* may be most similar to the extant *C. perfectus*.

DISCUSSION

The very speciose genus *Copelatus* has been divided into informal species groups based on the number and type of longitudinal striae present on the elytron. These characters have yet to be adequately tested

as synapomorphies, but given the extreme size of the genus and lack of a phylogenetic hypothesis it is convenient to recognize these informal groupings of species for ease of communication (Balfour-Browne 1939).

Based on the number of elytral striae, *Copelatus aphroditae* is rather isolated within *Copelatus*. The maximum number of elytral striae in *Copelatus* is typically 13 or less, with the extant South American *C. abomenci* Guignot being the only known exception thus far. This species has 22 dorsal striae plus one submarginal stria (Guéorguiev 1968; Guignot 1939). It has been historically placed in a group of its own, the *C. abomenci*-group, which was defined as having 14–23 striae (Guignot 1939). This is somewhat confusing since *C. abomenci* is the only species of the group and it has 23 striae. Therefore, we redefine the *C. abomenci*-group as those *Copelatus* with a total of 23 elytral striae. We assign *Copelatus aphroditae* to a new species group, the *C. aphroditae*-group, which is characterized by having 19 dorsal striae anteriorly on the elytron, and no obvious submarginal one.

Copelatus predaveterus belongs to the group with eleven sutural and one submarginal elytral striae (*Copelatus*-group 13 *sensu* Sharp (1882) and *trilobatus*-group *sensu* Guéorguiev (1968)). Other members of the *C. trilobatus*-group are tropical and occur in South America, Africa, southeast Asia and Australia. New World members occur primarily in northern South America and their habits are essentially unknown. However, other Copelatinae, such as *Aglymbus bromeliarum* Scott and *A. bimaculatus* Resende and Vanin, are known from Bromeliaceae (e.g. Resende and Vanin 1991). The unusual situation of having aquatic beetles entrapped in tree resin could be explained by their living in bromeliads, tree holes or other similar arboreal aquatic habitat. However, this is certainly speculative, and there are other possible explanations such as entrapment during dispersal or interment in resins deposited in the water. The fact that

the dytiscids from amber from very disparate localities and time periods are congeneric suggests that *Copelatus* may show a greater potential for becoming interred in amber, possibly because of specialized habitat preferences. Other inclusions in the Dominican amber pieces are terrestrial including several collembolans and a terrestrial hemipteran.

The age of Dominican amber has been controversial, but recent estimates place much of it at 15–20 million years (late Early to early Middle Miocene) (Iturralde-Viñe and MacPhee 1996) with others placing it at as much as 23–30 million years (Lower Miocene to mid Oligocene) (Grimaldi 1995). Baltic amber appears to be much older, and recent authors place it at some 40–55 million years (Eocene) (Michelsen 2000; Weitschat and Wichard 1998).

Little has been proposed regarding the phylogeny of Copelatinae. The striate *Copelatus* species appear to be monophyletic (Balke 2001), but relationships within this clade are not yet known. However, an upcoming molecular phylogenetic study of Copelatinae (Balke, Ribera & Vogler, in preparation) will likely help clarify the phylogeny of this diverse group. When attempting to propose potential historical explanations for diversity, it is crucial to reliably calibrate at least some nodes of cladograms used to infer divergences. Indirect, biogeographic evidence suggests a Gondwanian origin of Copelatinae, earlier than perhaps 120 mya (Balke 2001). Here, we present for the first time evidence for an origin of the more derived, striate forms of the genus predating perhaps 50 mya, a conclusion that will aid substantially any future studies of the evolution of this old and diverse group of beetles.

OTHER FOSSIL *COPELATUS*

Our new species are the first Copelatinae species described from amber and one, *C. aphroditae*, is the oldest fossil copelatine known. Three other fossil species in this genus have been described from well-pre-

served impression fossils from the middle Miocene (10–15 mya) in Northern Caucasian layers (Říha 1974):

Copelatus stavropolitanus Říha, 1974: eleven elytral striae (*C. nigrolineatus*-group).

Copelatus ponomarenkoii Říha, 1974: six elytral striae plus one submarginal stria (*C. irinus* group).

Copelatus fossilis Říha, 1974: ten elytral striae plus one submarginal stria (*C. erichsoni* group).

Copelatus species similar to these do not currently occur in this area. The closest extant relatives of these species are probably Afrotropical and/or Oriental.

ACKNOWLEDGMENTS

KBM thanks especially Dr. D. A. Grimaldi (American Museum of Natural History) for providing the opportunity to describe these specimens, for preparing the material and for much useful information about amber. KBM also thanks Dr. Q. D. Wheeler for advising him on this and other projects. MB thanks Dr. Fritz Hieke and Dr. E. Pietrezeniuk (Natukundemuseum Berlin, Paleontology) for advice on the Berlin amber collections. Dr. W. Weitschat (Hamburg) and Mr. Carsten Gröhn (Glinde) are thanked for the incredible opportunity to study the material under their care. Financial support of the FAZIT foundation (Frankfurt/Main, Germany) is greatly acknowledged.

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